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Taxonomic decomposition of the latitudinal gradient in species diversity of North American floras

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Abstract

Aim: To test the latitudinal gradient in plant species diversity for self-similarity across taxonomic scales and amongst taxa. *Location:* North America. *Methods:* We used species richness data from 245 local vascular plant floras to quantify the slope and shape of the latitudinal gradients in species diversity (LGSD) across all plant species as well as within each family and order. We calculated the contribution of each family and order to the empirical LGSD. *Results:* We observed the canonical LGSD when all plants were considered with floras at the lowest latitudes having, on average, 451 more species than floras at the highest latitudes. When considering slope alone, most orders and families showed the expected negative slope, but

31.7% of families and 27.7% of orders showed either no significant relationship between latitude and diversity or a reverse LGSD. Latitudinal patterns of family diversity account for at least 14% of this LGSD. Most orders and families did not show the negative slope and concave-down quadratic shape expected by the pattern for all plant species. A majority of families did not make a significant contribution in species to the LGSD with 53% of plant families contributing little to nothing to the overall gradient. Ten families accounted for more than 70% of the gradient. Two families, the Asteraceae and Fabaceae, contributed a third of the LGSD. *Main Conclusions:* The empirical LGSD we describe here is a consequence of a gradient in the number of families and diversification within relative few plant families. Macroecological studies typically aim to generate models that are general across taxa with the implicit assumption that the models are general within taxa. Our results strongly suggest that models of the latitudinal gradient in plant species richness that rely on environmental covariates (e.g. temperature, energy) are likely not general across plant taxa.

Keywords: Asteraceae, diversity, Fabaceae, gradient, latitude, species richness, taxonomic scale

Introduction

The canonical pattern for the latitudinal gradient in species diversity (LGSD), where species richness of a taxon or functional group is highest in the tropics and decreases with distance from the equator, is one of the most commonly observed patterns in biogeography (Hillebrand, 2004; Mittelbach et al., 2007; Willig, Kaufmann, & Stevens, 2003). The generality of this pattern across taxonomic groups, regions and time begs a general, macroecological explanation (Brown, 1995; Rohde, 1992; Rosenzweig, 1995).

Numerous explanations for the canonical LGSD have been proposed (see reviews in: Fischer, 1960; Gaston & Blackburn, 2000; MacArthur, 1972; Pianka, 1966), yet there is little consensus on the relative importance of the processes that generate and maintain this pattern (Gaston & Blackburn, 2000; Latham & Ricklefs, 1993; Weiser et al., 2007, 2017; Willig et al., 2003). Several factors may explain this lack of consensus. First, any diversity gradient is ultimately driven by spatial differences in the rates or sums of diversification (e.g. Cardillo, Orme, & Owens, 2005; Mittelbach et al., 2007) and range size and range dynamics (Janzen, 1967; Stevens, 1989; Weiser et al., 2007) and multiple combinations of these processes can generate observed patterns of diversity. Second, empirical reports of the shape and steepness of LGSDs vary in spatial extent and grain (reviewed in Hillebrand, 2004), and, importantly for this effort, across taxonomic resolutions from species within a single genus (e.g. Stevens & Enquist, 1998) to polyphyletic functional groups (e.g. 'woody plants' Weiser et al., 2007) to phyla (e.g. vascular plants in Kreft & Jetz, 2007). Third, there are taxa with non-canonical patterns of species richness that pervade the LGSD literature, but these groups are typically treated as anecdotal exceptions (Kindlmann,

Schödelbauerová, & Dixon, 2007). Plant families such as the Pinaceae and Poaceae (Stevens & Enquist, 1998; Visser, Clayton, Simpson, Freckleton, & Osborne, 2014), and insects such as the parasitic wasp taxa Ichneumonidae and Symphyta (Kouki, Niemelä, & Viitasaari, 1994; Owen & Owen, 1974) show peak species richness outside the tropics. Note that these taxa are taxonomic subsets of larger groups that show canonical LGSDs: vascular plants (Kreft & Jetz, 2007; Weiser et al., 2007) and insects (Weiser et al., 2017).

While the pattern is described across latitudes, the putative explanations of the LGSD do not attribute the gradient purely to latitude. Thus, attempts at macroecological explanations for LGSDs typically focus on covariates of latitude [e.g. habitat area (e.g. Rosenzweig, 1995; Terborgh, 1973), climate (e.g. Currie et al., 2004), available energy (e.g. Currie, 1991; Kaspari, Ward, & Yuan, 2004), distance to a dispersal boundary (e.g. Colwell & Hurtt, 1994), time since deglaciation. (Hawkins & Porter, 2003)] or on how these covariates interact with ecological and evolutionary traits (e.g. speciation rates Allen, Brown, & Gillooly, 2002) and/or effective evolutionary time (e.g. Rohde, 1992; Weiser et al., 2017) of the taxon under study. Macroecological explanations for the LGSD also often make the implicit assumption that these covariates of latitude are not taxon scale-dependent, at least not amongst the taxonomic scales (e.g. the 'Formicidae') and functional groups (e.g. 'trees') used in such studies. For example, the area of a continent and/or the temperature of a habitat is independent of the taxonomic rank of the focal taxon. We use this assumption to generate our null expectation that phylogenetically nested clades should show LGSDs similar in sign and shape of the more inclusive clades (e.g. plant families should show the same patterns as all plants).

Here we take a different approach. Accepting that LGSDs are not generated by latitude itself, but by spatial abiotic and biotic covariates of latitude, we: (1) describe an empirical LGSD for vascular plants from 245 comprehensive floristic treatments from Mexico, United States and Canada; (2) examine the slope and shape of the LGSD for each plant order and family separately; (3) investigate how gradients of two higher taxonomic levels (families and orders) influence the LGSD (i.e. adding a plant order to a flora adds at least one family and at least one species, by definition); and (4) calculate the contribution of each plant family to the overall LGSD. Thus, we fix the spatial extent of the analysis and vary taxonomic scale and scope. Noting previous published exceptions (e.g. Stevens & Enquist, 1998; Visser et al., 2014), we start with the expectation that plant taxa will show qualitatively similar canonical LGSDs across taxonomic scales. Thus, we are testing the implicit null models of self-similarity (i.e. LGSDs are similar across the taxonomic hierarchy) and generality (i.e. at a given taxonomic scale, LGSDs should be similar to each other).

Materials and Methods

Data

We used the complete list of plant species from all of the 245 floras used in McLaughlin (2007) who selected species lists from published floras to provide 'a uniformly distributed sample of landscapes from throughout' Mexico, the United States and Canada (see Figure 1) to describe the LGSD for these sites and taxa. The data set includes 18,710 species which we used genus name to assign each species to 241 monophyletic families and 65 monophyletic orders (Angiosperm Phylogeny Group, see <http://www.mobot.org/MOBOT/research/APweb/>). The number of species per order varies from 1 to 2,709 (mean = 299, median = 62), and the number of species per family varies from 1 to 2,615 (mean = 80.6, median = 15). These floras represent different biomes and floristic provinces and vary in topography, climate and areal extents. It is important to reiterate that this analysis is a comparison of patterns observed for taxonomic subgroups with the pattern for all taxa as the overarching null expectation. Also, as this analysis is primarily a comparison of patterns within and amongst plant orders and families occurring in local floras, the distribution of how this data set spatially 'samples' plant families is identical for the families considered. Thus, while the points are not spatially independent, any spatial interdependence is shared across families. Similarly, all plant families share the differences between the areas used to generate the flora such as spatial bias in area or elevation included or effort expended in the study areas. Original data sources, the list of floras and the raw data are in Appendices S1-S3.

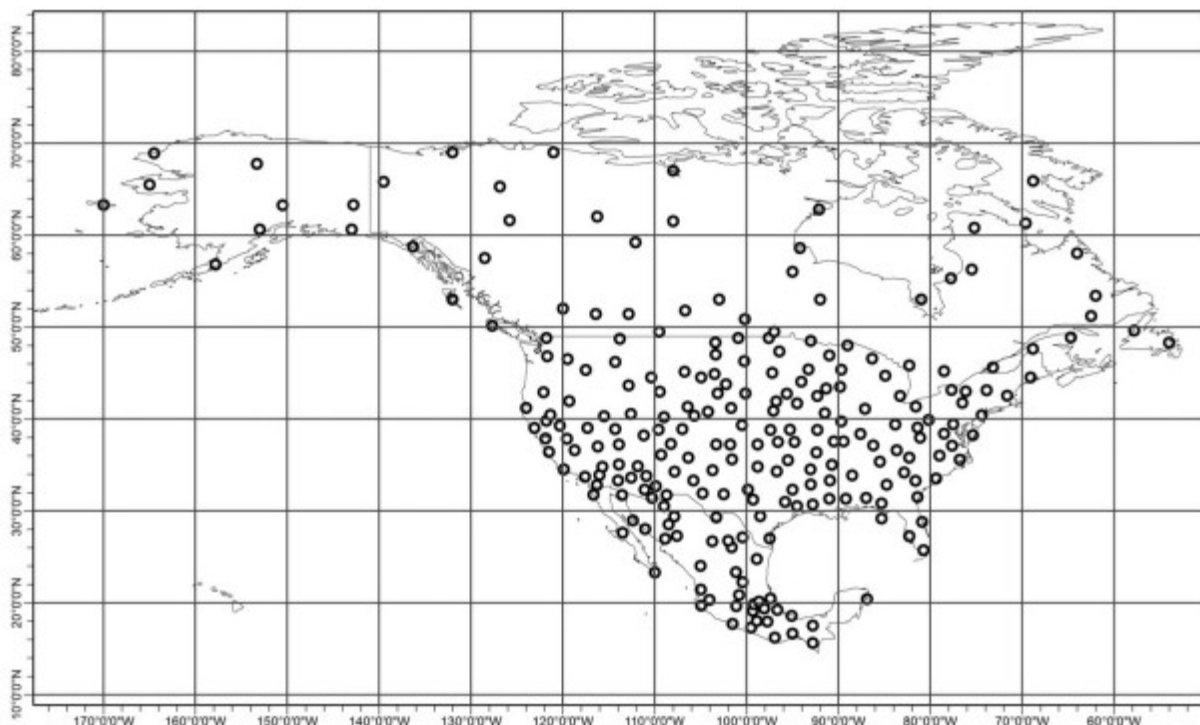


Figure 1. Locations of the 245 floras analysed

Is there self-similarity in strength and shape of the LGSD of families and orders?

Our null model is that families and orders should show LGSDs similar to the overall LGSD for all plants. We do not argue that this must be exact self-similarity where an observed % decrease in species diversity of all plants necessitates an identical % decrease in the species diversity of each family. We do argue that a minimal self-similarity would be to show a significant decrease in species richness and a similar functional form of the overall LGSD, mirroring the sign of the slope and the shape of the overall pattern.

To describe the slope and shape of the overall LGSD, we performed standard linear and quadratic regression of the total number of vascular plant species, families and orders found in each flora against latitude (data in Appendix S2). We repeated this procedure for the number of species within each plant family and order, thus generating a LGSD for each higher taxon. Zeros (i.e. no species within a given taxon found in a given flora) are retained and included in the family- and order-level analyses. As using zeros may affect the nature and significance of the LGSD, especially for narrowly distributed taxa, we also ran linear and quadratic models as above omitting sites with zero species for the taxon at hand. As low species richness can constrain the slope (i.e. the units are species per degree latitude, 'spd') of the LGSD, we also performed these regressions on richness rescaled to the highest observed species richness of that taxon (S_{\max}) extracting slopes in units relative to maximum richness $[(S/S_{\max})/^\circ\text{latitude}]$. Multiplying this slope by 100 gives the proportional changes in per cent of maximum diversity change per degree latitude ('%max'). Thus, for each family and order, we have two measures of slope: species per degree change and proportional change. The rescaling procedure does not alter the curvature (quadratic term) of the quadratic regression.

How does the diversity of families and orders affect the LGSD?

All species in the data set belong to (assumed monophyletic, at least with regards to the other taxa in the analysis) families and orders. Therefore, latitudinal patterns in the diversity of higher taxa should affect patterns of species diversity. To test for this, we used a series of generalized linear models (Poisson with log-link) using all combinations of latitude, the number of families (F) and orders (O) present on species diversity (S). We did not test for interaction effects. We used the Akaike information criterion (AIC) to compare the performance of the different models, where we retain additional parameters that improve the model when $\Delta\text{AIC} \geq 2$.

How much does each taxon contribute to the LGSD?

To quantify the family-level contribution to the overall LGSD, we subtracted the species richness predicted by each family-specific regression model at 69° N from the species richness predicted by that regression model at 15.6°

N (the latitudinal extent of our data set). Thus, if a slope is not significantly different from zero, the regression model predicts zero difference in species richness across these latitudes and we consider that taxon to contribute zero species to the overall LGSD. If the model predicts 100 species at 15.6° N and 10 species at 69° N then we consider that family to have contributed 90 species to the overall LGSD.

Results

Description of the empirical diversity gradients

On average, species richness of floras decreases with increasing latitude (Figure 2a). Flora species richness decreases, on average, 8.4 species per degree of latitude ($S = 905 - 8.4 * \text{Latitude}$, $r^2 = .19$, $n = 245$, $p < .001$). While there is considerable scatter, this model generates a specific empirical LGSD that predicts 778 species, on average, at 15.6° N and 327 species 69° N (the latitudinal limits of our data set). Thus, the latitudinal gradient in species diversity is 451 species. When modelled as a quadratic regression, species diversity is relatively flat until around 40° N where it decreases rapidly (dashed curve in Figure 2a; $S = 512.3 + 12.4 * \text{Latitude} - 0.25 \text{Latitude}^2$, $r^2 = .23$, $n = 245$, $p < .001$).

The slope of the LGSD varies amongst families and orders

Most of the orders (47 orders, 72%) and families (167 families, 69%) showed the canonical LGSD with a significant negative slope (Table 1 and Table S2 in Appendix S1). The steepest negative proportional changes (in units of per cent of peak diversity) were found in the orders Oxalidales (−1.1%), Commelinales (−1.1%), Solanales and Gentianales (both −1%). The steepness of the LGSD for these orders is likely driven by family-level patterns, as three of these orders have families with the steepest negative proportional changes: Apocynaceae (−1.1%), Oxalidaceae (−1.05%) and Commelinaceae (−1.05%).

The most negative per degree changes (in units of species per degree latitude, 'spd') are in the two most diverse orders, Asterales (−1.5 spd) and Fabales (−1.4 spd). This is likely due to the numerically dominant families Asteraceae (−1.5 spd) and Fabaceae (−1.3 spd) having the steepest species per degree changes at the family level. These two families also have the highest species diversity across this data set (Asteraceae 2615 spp.; Fabaceae 1492 spp.).

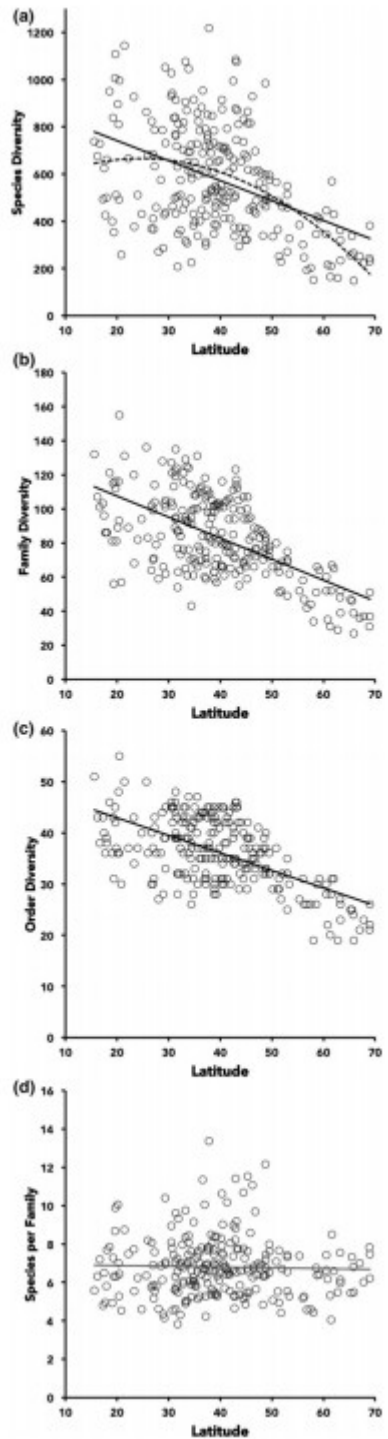


Figure 2. Patterns of diversity for the 245 vascular plant floras plotted against latitude for North America. Flora species (a) family (b) and order (c) diversity decreases with latitude (species diversity = $910.5 - 8.45\text{Latitude}$, $r^2 = .19$; family diversity = $132 - 1.2\text{Latitude}$, $r^2 = .36$; order diversity = $49.8 - 0.34\text{Latitude}$, $r^2 = .35$; all $p < .001$). Dashed line in (a) is the quadratic fit ($S = 512 + 12.4\text{Latitude} -$

0.25Latitude^2 , $r^2 = .23$). The number of species per family present does not vary with latitude (d; grey line is $S/O = 6.96$, $p = .628$)

Table 1. Results of regression analyses of families and orders discussed in the text (see Table S2 in Appendix S1 for complete results). S is the number of species in the entire data set for each taxon; ImSPD is the slope of the linear model in units of species per degree latitude; lummox is the slope of the linear model rescaled to maximum species richness in units of per cent of maximum diversity per degree latitude (also see methods). For both linear model slopes, negative values indicate the canonical LGSD with higher species richness at lower latitudes, and positive values indicate reverse LGSDs. $\text{Im } r^2$ and $\text{quad } r^2$ are the coefficient of determination for the linear and quadratic models, respectively. quad is the quadratic term from the quadratic regression (the quadratic term does not change with rescaling relative to S_{max}), with negative values indicating the concave functional form (i.e. 'hump shaped') and positive values indicating the convex functional form (i.e. 'U-shaped'). S_{contr} is the number of species a given taxa adds to (or subtracts from) the canonical LGSD. 'ns' indicates that the coefficient or whole model is not significant at $p < .05$

Order	Family	S	lmSPD	lm%max	lm r^2	quad	quad r^2	S_{contr}
Alismatales	All Alismatales	181	ns	0.21	–	–0.01	0.07	–4.7
	Juncaginaceae	7	0.03	1.03	0.22	ns	0.21	–1.6
Apiales	Apiaceae	299	ns	ns	–	–0.016	0.26	3.3
Asparagales	All Asparagales	784	–0.41	–0.32	0.11	0.014	0.14	21.6
	Asparagaceae	148	–0.12	–0.89	0.31	0.003	0.35	6.6
	Orchidaceae	553	–0.23	–0.21	0.04	0.013	0.07	12.2
Asterales	All Asterales	2,709	–1.54	–0.74	0.23	–0.07	0.35	81.9
	Asteraceae	2,615	–1.53	–0.76	0.24	–0.07	0.35	81.2
Boraginales	All Boraginales	479	–0.21	–0.41	0.06	–0.014	0.12	11.4
	Boraginaceae	289	–0.14	–0.41	0.06	–0.007	0.10	7.1
	Hydrophyllaceae	186	–0.08	–0.29	0.04	–0.007	0.12	4.1
Brassicales	All Brassicales	423	0.16	0.32	0.05	–0.009	0.08	–8.7
	Brassicaceae	356	0.24	0.48	0.11	–0.01	0.16	–12.7
Caryophyllales	All Caryophyllales	1,282	–0.47	–0.38	0.08	ns	0.08	24.8
	Amaranthaceae	216	–0.15	–0.51	0.09	–0.005	0.12	7.8
	Cactaceae	379	–0.32	–0.72	0.25	0.007	0.27	17.2
	Caryophyllaceae	190	0.22	0.80	0.21	0.004	0.22	–11.5
	Polygonaceae	269	ns	ns	–	–0.015	0.24	–0.7
Commelinales	All Commelinales	110	–0.16	–1.07	0.45	0.005	0.56	8.6
	Commelinaceae	108	–0.16	–1.05	0.44	0.005	0.55	8.4
Equisetales	Equisetaceae	12	0.13	1.43	0.47	–0.001	0.48	–6.8
Ericales	All Ericales	652	0.22	0.36	0.04	–0.009	0.06	–11.8
	Ericaceae	183	0.35	0.91	0.19	ns	0.19	–18.3
	Polemoniaceae	222	ns	ns	–	–0.01	0.11	2.8
Fabales	All Fabales	1,576	–1.42	–0.84	0.47	0.02	0.49	75.1
	Fabaceae	1,492	–1.33	–0.83	0.45	0.02	0.48	70.3
Gentianales	All Gentianales	746	–0.66	–1.03	0.41	0.009	0.43	35.0
	Apocynaceae	280	–0.30	–1.11	0.44	ns	0.44	15.9
	Gentianaceae	106	ns	ns	–	ns	–	–0.8
	Rubiaceae	345	–0.35	–0.74	0.34	0.009	0.39	18.5
Lamiales	All Lamiales	1,564	–1.00	–0.96	0.35	–0.014	0.36	53.2
	Lamiaceae	378	–0.30	–0.86	0.21	–0.01	0.27	16.0
Liliales	All Liliales	400	ns	–0.17	–	–0.03	0.19	3.9
	Liliaceae	365	ns	ns	–	–0.016	0.19	0.8
Malpighiales	All Malpighiales	987	–0.55	–0.42	0.20	ns	0.20	29.4
	Euphorbiaceae	500	–0.62	–0.73	0.45	0.012	0.49	33.0
	Salicaceae	119	0.31	1.15	0.39	ns	0.38	–16.5
Malvales	All Malvales	375	–0.48	–0.70	0.43	0.014	0.52	25.4
	Malvaceae	329	–0.43	–0.68	0.40	0.015	0.51	23.0

Order	Family	S	lmSPD	lm%max	lm r^2	quad	quad r^2	S_{contr}
Oxalidales	All Oxalidales	46	-0.07	-1.09	0.27	ns	0.27	3.5
	Oxalidaceae	36	-0.05	-1.05	0.19	-0.0009	0.20	2.8
Pinales	All Pinales	125	ns	ns	-	-0.006	0.07	-0.9
	Pinaceae	88	ns	ns	-	-0.004	0.04	-0.5
Poales	All Poales	2,151	ns	ns	-	-0.103	0.15	-7.0
	Bromeliaceae	123	-0.15	-0.53	0.26	0.01	0.52	8.1
	Cyperaceae	778	0.66	0.44	0.07	-0.05	0.17	-35.0
	Juncaceae	130	0.17	0.61	0.12	-0.01	0.22	-9.1
	Poaceae	1,079	-0.55	-0.46	0.07	-0.05	0.22	29.3
Polypodiales	All Polypodiales	479	-0.33	-0.39	0.10	ns	0.10	17.7
	Dryopteridaceae	101	0.08	0.41	0.04	-0.004	0.07	-4.4
	Pteridaceae	164	-0.21	-0.74	0.23	0.004	0.25	11.4
Ranunculales	All Ranunculales	337	0.29	0.60	0.13	-0.02	0.28	-15.5
	Ranunculaceae	230	0.33	0.74	0.21	-0.02	0.34	-17.3
Rosales	All Rosales	597	ns	0.17	-	-0.03	0.17	-6.3
	Moraceae	55	-0.10	-0.45	0.23	0.006	0.40	5.5
	Rhamnaceae	96	-0.10	-0.78	0.27	ns	0.26	5.4
	Rosaceae	371	0.40	0.71	0.13	-0.03	0.35	-21.4
	Ulmaceae	23	-0.06	-0.69	0.11	-0.002	0.16	2.9
	Urticaceae	47	-0.06	-0.61	0.12	ns	0.13	2.9
Saxifragales	All Saxifragales	314	0.33	0.73	0.23	ns	0.23	-17.5
	Crassulaceae	119	-0.06	-0.42	0.13	ns	0.13	2.9
	Saxifragaceae	125	0.32	0.99	0.36	0.0034	0.37	-16.8
Solanales	All Solanales	496	-0.69	-1.04	0.56	0.0143	0.62	36.9
	Convolvulaceae	232	-0.30	-0.74	0.42	0.0062	0.47	16.1
	Solanaceae	264	-0.39	-0.93	0.53	0.0081	0.59	20.8

While a majority of plant families and orders show the expected pattern of higher tropical diversity, 30.4% of plant families and 22.6% of plant orders do not (Figure 3). Seven orders (11%) and 32 families (13%) show reverse LGSDs with significant positive slopes. The most positive proportional changes were found in the orders Equisetales (1.4%), Saxifragales (0.7%) and Ranunculales (0.6%). In addition to the mono-familial Equisetales (=Equisetaceae), the families with the steepest positive proportional changes were the Salicaceae (1.2%), Juncaginaceae (1.0%) and Saxifragaceae (1.0%, Saxifragales). The four orders with the most positive species per degree changes were the Saxifragales (0.33 spd), Ranunculales (0.29 spd), Ericales (0.22 spd) and Brassicales (0.16 spd), likely due to their numerically dominant families showing strong positive slopes (i.e. Saxifragaceae [0.32 spd, Saxifragales], Ranunculaceae [0.33 spd, Ranunculales], Ericaceae [0.35 spd, Ericales] and Brassicaceae [0.24 spd, Brassicales]). The two families with the most positive species per degree changes, the Cyperaceae (0.66 spd) and the Rosaceae (0.40 spd), were from orders that did not have a significant positive gradient (Poales and Rosales).

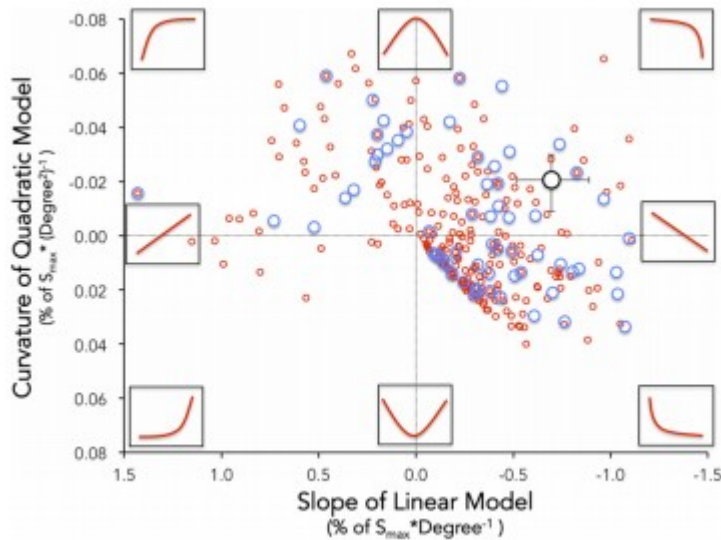


Figure 3. The slope and curvature of the LGSD for family (red circles), order (larger blue circles) and the entire data set (black circle) with black error bars indicating the 95% confidence intervals for slope and curvature for the entire data set. Here coefficients are in units of % of the maximum observed single-flora species diversity to control for overall taxon diversity. The eight small insets are cartoons of the LGSD shape for the combinations of linear and quadratic terms. Taxa found to the right of 0.0 show various functional forms and magnitudes of the canonical LGSD, while taxa found to the left show reverse LGSDs. Taxa with quadratic terms <0.0 have 'concave down' shaped LGSDs, while those with quadratic terms >0.0 have 'convex up' shaped LGSDs. Taxa with quadratic terms around zero have linear LGSDs.

Of the 65 orders and 241 families evaluated, 11 orders (11.6%) and 42 families (17.4%) do not show linear diversity gradients (i.e. the regression slope was not significantly different from zero, Figure 4, Table 1, and Table S2 in Appendix S1). While many of the families and orders with no significant slope are not diverse (two of these orders and 22 of these families have fewer than five species in the data set), this group includes diverse orders such as Poales (2,151 spp.), Rosales (597 spp.) and Liliales (400 spp.) and families such as Liliaceae (365 spp.), Apiaceae (299 spp.) and Polygonaceae (269 spp.).

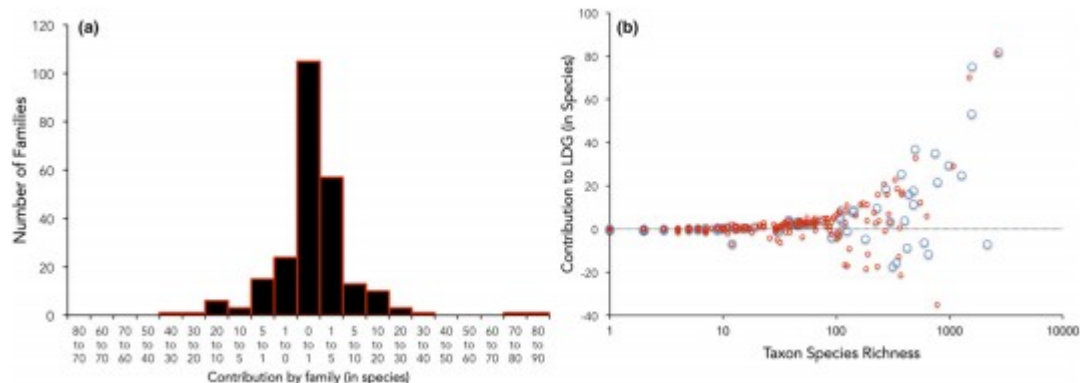


Figure 4. Most families contribute little to the overall species diversity gradient. (a) Histogram of the number of families that contribute (or subtract) a given number of species to the overall LGSD. Right of zero indicates a positive contribution to the canonical LGSD, while left of zero indicates a negative contribution (i.e. a reverse LGSD). Note unequal bin sizes. (b) Family (red circles) and order (larger blue circles) contribution to the overall LGSD as a function of the number of species from that family (in these data). The dotted line represents zero contribution to the LDG, points above the line represent a positive contribution to the gradient (i.e. these families have more species in the tropics), and points below the line represent 'reverse LDGs' where families have fewer tropical species.

Removing sites that have zero species for a given taxon greatly affected the number of the families that has significant slopes. Of the 167 families with a significant and negative slope, more than half (90 families) did not have a negative slope when zeros were removed (See Tables S2 and S3). Seventeen families with reverse LGSDs did not have a significant slope with zeros removed. That 107 families went from significant to not significant slopes points to the importance of including absences in this data set, and all further results and discussion are from analyses including absence data (but see Table S2 in Appendix S1 for results with absences removed). That said, these taxa typically had a very low contribution to the overall LGSD even when their slopes were significant. Taxa that went from significant to not significant slopes would be expected to have highest diversity nearer the extreme latitudes. Within the 91 taxa that had qualitatively similar results for both methods, 58 (66%) showed steeper slopes with the zeros removed, showing that they may have significant structure within their ranges.

The shape of the LGSD varies amongst families and orders

The curvature of the overall LGSD is concave downward (i.e. the quadratic term is negative) and asymmetrical for these data (Figure 2a, also see the black circle in Figure 3). Using quadratic regression, flora at the northern limit of the data have, on average, 55.7 species, while flora at the southern limit have, on average, 412.5 species (dashed line in Figure 2a). Assuming self-similarity across taxonomic scales, we expect orders and families will show significant negative slopes (i.e. show the asymmetry) and have negative quadratic terms (i.e. be a concave-down).

Using a strict expectation of the functional form of the LGSD, less than half of the orders (26 of 65, 38.5%) and families (92 of 241, 38.2%) show both significant and positive linear and quadratic terms (Figure 3). Removing the expectation of shape, three quarters of orders (47 of 65, 72.3%) and families (167 of 241, 69.3%) show a canonical LGSD with a tropical peak that decreases with latitude.

Of the 65 orders, 24 (37%) have significant and negative quadratic terms (i.e. they are concave down), but 10 of these (42% of the 24 concave-down orders) do not show the asymmetry expected—they are 'hump-shaped' LGSDs. Twenty-six orders (40%) show both a significant positive quadratic term and negative linear term, meaning they have highest species diversity

at the southern end of the gradient that drops quickly and remains low for the remainder of the gradient (bottom right quadrat of Figure 3). Of the 15 orders with no curvature to their LGSD, most (12, 18.5% of all orders) showed negative slopes, while 2 (3% of all orders) showed linear reverse LGSDs.

Of the 241 families, 32 (13%) showed significant and negative linear and quadratic terms. There were 20 families (8%) that showed the expected negative quadratic term but a positive slope, thus a reverse LGSD that is a mirror image of the overall LGSD. There were 21 (8.7%) families with 'hump-shaped' LGSDs. There were 92 (38%) families show both a significant positive quadratic term and negative linear term. Three families show both quadratic and linear terms significantly positive, meaning their diversity is flat at the southern end of the gradient and increases sharply at the northern end. There were 43 (17.8%) families that have linear LGSDs with the expected negative slope but no curvature. There were nine (3.7%) families that show linear reverse LGSDs.

Families, not orders are predictive of species diversity

Average family (F) and order (O) diversity decrease with increasing latitude. Family diversity decreases, on average, from 112 families per flora at 15.6° N to 47 families per flora at 69° N (Figure 2b; $F = 132.2 - 1.23 \times \text{Latitude}$, $r^2 = 0.36$, $n = 245$, $p < .001$). Similarly, order diversity decreases, on average, from 44.4 to 26.1 orders per flora (Figure 2c; $O = 49.8 - 0.34 \times \text{Latitude}$, $r^2 = .35$, $n = 245$, $p < .001$). The number of species per family does not vary with latitude (Figure 2d; $S/F = 7$, $p = .63$).

Of the single parameter generalized linear models, the number of families F was the best predictor of S , while latitude was worst (Table 2). Adding O to the model with F did not significantly decrease AIC, and the parameter estimate for O was not significantly different from zero (Table 2). Even though family and order diversity are highly correlated ($O = 13.5 + 0.27F$, $r^2 = .93$, $n = 245$, $p < .001$), the number of orders O is never predictive of S when the number of families F is included in the model. While latitude by itself was a poor predictor of S , latitude and number of families F produced the model that best predicted species richness S (Table 2).

Different families contribute differently

While these data are drawn from descriptive floras that vary in area, climate, floristic provinces, etc., we are able to describe an empirical, canonical LGSD that varies, on average, by 451 species across 53 degrees of latitude.

Table 2. Model comparisons of generalized linear models using latitude, the number of orders (O) and the number of families (F) per flora to predict flora species richness. '-' indicates that the parameter was not included in that model, 'ns' indicates that parameter estimate is not significant at $p < .05$

	Latitude	Orders	Families	r^2	AIC
Lat.	-0.015	–	–	.19	20,133
O	–	0.048	–	.62	10,358
F	–	–	0.014	.69	9,285
F+O	–	ns	0.013	.69	9,286
Lat+O	ns	0.048	–	.62	10,360
Lat+F	-0.002	–	0.014	.69	9,254
Lat+F+O	-0.002	ns	0.014	.70	9,255

The number of species per family varies considerably across plant families (i.e. from 1 to 2,615), as do the slopes of the family-level LGSDs. Thus, families contribute to the overall LGSD differently. On average, families contribute fewer than two species to the overall gradient (mean \pm SD = 1.9 \pm 9.2 species). That said, most families contribute less than one species across the 53° latitudinal gradient we examine (mode = 0.06 species, median = 0.38 species). One hundred and twenty-nine of the 241 families contribute between –1 and 1 species to the overall LGSD (Figure 4a).

The two families with the most species in the data set also contribute the most species to the overall LGSD. Asteraceae (2,615 spp.) contributes 81 species to the LGSD, and Fabaceae (1,492 spp.) contributes 70 species. The ten most species-rich families (i.e. Asteraceae, Fabaceae, Euphorbiaceae, Poaceae, Malvaceae, Solanaceae, Rubiaceae, Cactaceae, Convolvulaceae, Lamiaceae and Apocynaceae) contribute 341 species to the overall LGSD. Thus, 4% of families contribute 75% of the increase in species diversity along this gradient.

Discussion

This LGSD is a consequence of family diversity and diversification of a few families

The latitudinal gradient in plant species diversity that we describe here is an amalgam of two latitudinal gradients: the first in plant family diversity and the second in species diversity of a minority of plant families. The most common functional form of LGSD described here is high tropical diversity with little to no representation in the temperate zone (i.e. concave up with a negative slope, Figure 3), indicating that most families are tropical taxa that cannot or have not been able to extend into and/or diversify at temperate latitudes. This is consistent with the tropical conservatism hypothesis (TCH), where families that arose in the humid, warm tropics have not evolved adaptations to dry or cold habitats at higher latitudes (Kerkhoff, Moriarty, & Weiser, 2014; Weiser et al., 2007; Wiens & Donoghue, 2004). Also consistent with the TCH is the observation that many (90) families that showed the expected negative slope did not have statistically significant slopes when sites with zero species in that taxon were excluded (Table S3). This pattern describes families that are only found at lower latitudes, but do not vary systematically with latitude where they occur.

Models of species diversity that include family diversity are highly predictive, and the addition of latitude, while improving the model, does not alter the parameter estimate for family diversity. The number of families per flora decreases, on average, by 65 families across the latitudes we studied (i.e. from 15.6° N to 69.0° N). Adding a family to a flora automatically adds, at minimum, one species to a flora, thus the minimum contribution of family diversity to this LGSD is 65 species, or about 14% of the empirical LGSD.

The contribution of species difference to the LGSD of relatively few families outweighs the impact of family diversity. For these data, a vast majority of plant families contributed little to the overall LGSD (and those with reverse LGSDs counter the expected pattern). The families Asteraceae and Fabaceae contribute 152 species to the LGSD and thus <1% of the plant families contribute a third (34%) of the increase along this LGSD. The 10 families with the largest contributions explain 72% of the increase along this gradient (325 species).

To quantitatively impact the LGSD, a taxon must be species rich (Figure 4b, Kreft & Jetz, 2007; Kreft, Jetz, Mutke, Kier, & Barthlott, 2008) and that diversity must vary across latitudes. While diverse taxa did impact the LGSD the most, diversity was necessary but not sufficient for strongly influencing the LGSD (Figure 4b). Diverse orders such as the Poales (2,151 spp.) and Rosales (597 spp.) and families Liliaceae (365 spp.) and Apiaceae (299 spp.) did not have significant LGSDs.

The LGSD is not a general pattern across taxa nor taxonomic scale

The LGSD in the Western Hemisphere is well supported for trees (Currie, 1991; Gentry, 1988; Latham & Ricklefs, 1993; Stevens, 1989; Weiser et al., 2007) as well as for vascular plant floras (Kreft & Jetz, 2007). While our data show the expected LGSD when all vascular plant species are considered together, this pattern is not general across plant orders or families nor across taxonomic scales.

For example, the relatively diverse order Poales does not mirror the overall pattern, as the species richness of Poales does not vary significantly with latitude. This lack of a significant gradient for the order Poales conceals and is perhaps due to the significant and opposing LGSDs for the four most diverse families of Poales. The Poaceae (1,079 spp.) and Bromeliaceae (123 spp.) both have negative slopes (-0.55 spd and -0.15 spd, respectively), while Cyperaceae (778 spp.) and Juncaceae (130 spp.) both show positive slopes (0.66 spd and 0.17 spd, resp.). Thus, the significant canonical LGSDs of Poaceae and Bromeliaceae are 'offset' by significant reversed LGSDs in the Cyperaceae and Juncaceae. Similarly, the Rosales shows no significant slope. The strong reverse LGSD of the Rosaceae (0.40 spd, 371 spp.) is likely offset by the remaining Rosales (Moraceae [-0.1 spd, 55 spp.], Rhamnaceae [-0.1 spd, 96 spp.], Urticaceae [-0.06 spd, 47 spp.] and Ulmaceae [-0.06 spd, 23 spp.]). It is possible, if not likely, that the diverse families with

no significant LGSD (e.g. Polygonaceae) have similar offsetting patterns at finer taxonomic grains.

Reverse LGSDs

Any hypothesis that predicts a canonical LGSD is effectively falsified (for that data and taxonomic scale) when the canonical LGSD is not observed.

Reverse LGSDs, while seen in only 10% of families in this data, argue even more strenuously against hypotheses that predict the canonical LGSD. While only 32 families showed significant reverse LGSDs, it is important to remember that there is a latitudinal gradient in family diversity, with only 47 families per flora, on average, at the northern limits of our data.

If patterns are not general, then what does this say about process?

That at least 10% of the LGSD described here can be attributed to the distribution of plant families that cannot, or at least have not, occupied higher latitudes is consistent with 'Tropical Conservatism' being important to the overall LGSD. The magnitude of this effect is partially counterbalanced by 'Temperate Conservatism' where families cannot or have not occupied lower latitudes (and thus show a reverse LGSD). There are several families that are relatively diverse that show no difference in diversity across these latitudes (e.g. Liliaceae, Apiaceae) for which phylogenetic conservatism cannot be invoked in either direction (at least not at the scale of family).

Macroecological explanations for the canonical LGSD typically invoke the influence of environmental covariates of latitude on diversification processes to generate models to explain the observed pattern (Gaston & Blackburn, 2000; Willig et al., 2003). Taxonomic (or phylogenetic) decomposition of diversity gradients allows for falsification of such hypotheses for subsets of the larger group. For example, a model that asserts that the plant LGSD is generated by differences in diversification rates with environmental covariates (e.g. area, precipitation, elevation, see Kreft et al., 2008) would not explain the diversity patterns for both the Poaceae and Cyperaceae, as they show opposite patterns of diversity across latitudes.

This does not mean that there are not general or generalizable explanations for diversity gradients, but that working towards such general explanations will necessitate understanding the taxonomic- and phylogenetic-scale dependence of these patterns as well as the biogeographical and phylogenetic history of the taxon of interest. For example, the diversification rates for the Cyperaceae (which has a reverse LGSD) increased an order of magnitude with global cooling, and thus the expansion of the temperature zone, after the Late Eocene/Oligocene (Escudero, Hipp, Waterway, & Valente, 2012). The Fabaceae, with a canonical LGSD, have had a family-wide, ongoing radiation, since the warmer Palaeocene (Lavin, Herendeen, & Wojciechowski, 2005).

Our results emphasize the tautology that a plant family must be diverse to contribute significantly to diversity gradients. Therefore, an important first

step would be to understand what evolutionary processes have led to the high-diversity families with significant LGSDs. Our results also show that high diversity, while necessary for, is not sufficient to show the canonical LGSD. Therefore, a second step would be to understand how biogeographical and evolutionary history interact to generate diverse families that do not show significant and/or reverse LGSDs. Lastly, understanding what drives diversity patterns at the scale of plant families (e.g. niche conservatism, dispersal limitation) would help account for at least 10% of this particular LGSD, while understanding what drives species diversity patterns within 10 plant families would account for three quarters of the latitudinal gradient in plant species diversity.

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BIO

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